

The Leaf Organization of *Kummerowia* (Leguminosae)

Yu IOKAWA, Tomoyuki NEMOTO and Hiroyoshi OHASHI

Biological Institute, Graduate School of Science, Tohoku University, Sendai, 980-77 JAPAN

(Received on March 18, 1996)

Leaves of *Kummerowia* have been described as palmate or as pinnate. In order to clarify the leaf organization, leaves of *Kummerowia* were examined morphologically and anatomically. Morphological observations revealed that rachis exists between the top of petiole and the pulvinus of terminal leaflet. The rachis differs from the pulvinus in having two ridges on the adaxial side and no wrinkle in surface. Though the rachis becomes shorter in upper leaves, it is clearly distinguished from the pulvinus by these external features. The leaf organization of *Kummerowia* is therefore regarded as being pinnately trifoliolate. Anatomical observations revealed that the leaf of *Kummerowia* has a similar vascular system to that in the pinnately trifoliolate leaves of other leguminous species. The leaf organization of *Kummerowia* is identical with those of its allied genera *Lespedeza* and *Campylotropis*.

The genus *Kummerowia* comprises two species, *K. striata* (Thunb. ex Murray) Schindler and *K. stipulacea* (Maxim.) Makino. These are naturally distributed in East Asia and have been introduced widely in North America. This genus is included in the subtribe Lespedezinae of the tribe Desmodieae together with allied genera *Lespedeza* and *Campylotropis* (Ohashi et al. 1981). Taxonomic treatments of these genera have been controversial (Nemoto and Ohashi 1988), and the relationships between them have been discussed on the basis of the floral nectary (Nemoto and Ohashi 1988), the inflorescence (Akiyama and Ohba 1985, Nemoto and Ohashi 1990, 1993, 1996, Nemoto et al. 1995) and restriction fragment length polymorphisms of chloroplast DNA (Nemoto et al. 1995). Akiyama and Ohba (1985) regarded *Kummerowia* as being distinct from other two genera based on the features of inflorescence, whereas Nemoto and Ohashi (1988, 1990, 1993, 1996) and Nemoto et al. (1995) showed that

Kummerowia has more closer relationship to *Lespedeza* than to *Campylotropis*.

Leaves are trifoliolate in those three genera and they have been usually described as pinnately trifoliolate in *Lespedeza* (Hutchinson 1964, Ohwi 1965, Isely 1990, Li and Chen 1995) and *Campylotropis* (Hutchinson 1964, Fu 1987, 1995). On the other hand, trifoliolate leaves of *Kummerowia* have been described as palmate (Watari 1934, Ohwi 1965, Hatusima 1975, Isely 1990) or as pinnate (Liu 1955, Yang and Huang 1995). According to Ohashi et al. (1981), leaves of the tribe Desmodieae are generally pinnately trifoliolate.

The pinnately trifoliolate leaf is distinguished from the palmately trifoliolate one by the presence of the rachis above the petiole (Hickey 1979). Because each leaflet has the pulvinus at the base throughout the Leguminosae (Dormer 1946), the petiole is connected by the rachis with the pulvinus of terminal leaflet in the pinnately trifoliolate leaf, while it is directly

connected with that in the palmately trifoliolate one.

Watari (1934) anatomically studied the vascular system in the petioles and rachises of many leguminous species and pointed out the difference in vascular system between the pinnately trifoliolate leaf and the palmately trifoliolate one. He regarded *K. striata* as having the vascular system in the palmately trifoliolate leaf.

In this paper, in order to clarify the leaf organization, we examined leaves of *Kummerowia* morphologically and anatomically.

Materials and Methods

Leaves of *Kummerowia striata* and *K. stipulacea* were examined. Typical palmately trifoliolate leaves of *Trifolium repens* L. were also examined for comparison. For morphological observations, herbarium specimens kept in TUS were investigated under a binocular microscope. Moreover, FAA-fixed leaves collected in the fields (Table 1) were dehydrated in an ethyl alcohol series, transferred to isoamyl acetate, dried in a critical point dryer, placed on aluminum stubs, coated with gold, and observed by a Hitachi S-4100 scanning electron microscope. For anatomical observations, FAA-fixed materials were dehydrated in a t-butyl alcohol series, embedded in paraffin and sectioned at a thickness of 10 μm with a rotary microtome. Sections were stained with safranin and fast green FCF and examined by a light microscope.

Observations

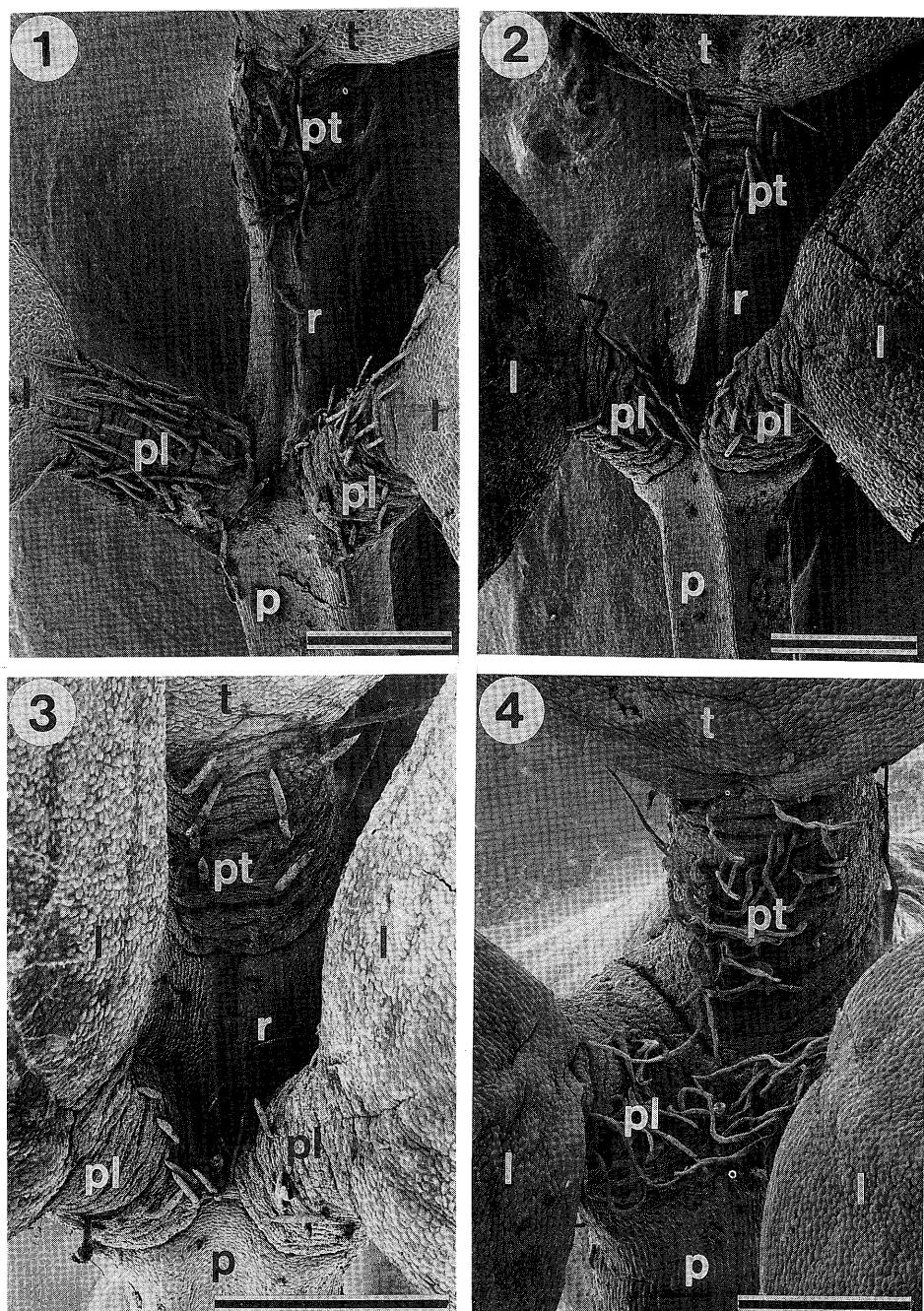
Morphological observation A leaf of *Kummerowia* comprises three leaflets. Each leaflet has a pulvinus at the base. We observed the rachis between the top of petiole and the pulvinus of terminal leaflet (Figs. 1, 2, 3). The pulvinus of terminal leaflet attaches on the top of the rachis, while that of the lateral leaflet attaches directly to the top of petiole. The rachis is clearly distinguished from the pulvinus by the following differences: the rachis has two ridges running along the adaxial side, slender outline and smooth surface, while the pulvinus has no ridges, but swollen outline and wrinkled surface. Moreover, the pulvinus falls down with the terminal leaflet when plants shed their leaflets, but the rachis remains at the top of petiole. The rachis varies in length, 0.2–1.4 mm long in *K. striata* and 0.1–0.8 mm long in *K. stipulacea*. Although it becomes shorter in upper leaves in both species (Figs. 3, 5), the rachis is clearly distinguished from the pulvinus by those different features.

Leaves of *Trifolium repens*, which represent a typical palmately trifoliolate leaf, don't have the rachis and the three pulvini of leaflets are attached directly to the top of petiole (Fig. 4). Leaves of *Kummerowia* are clearly different in structure from the palmately trifoliolate leaf.

Anatomical observation The rachis can be distinguished from the pulvinus of terminal leaflet by the shape of the transverse section in *K. striata* and *K. stipulacea*.

Table 1. A list of fresh and FAA-fixed materials examined. Voucher specimens are all kept in TUS

Taxa	Locality & Collector
<i>Kummerowia</i>	
<i>striata</i>	Japan, Miyagi Pref., Sendai, Y. Iokawa 5240.
	Japan, Fukushima Pref., Hobara-machi, Y. Iokawa 5238.
	Japan, Fukushima Pref., Yabuki-machi, Y. Iokawa 5242.
<i>K. striata</i>	Japan, Miyagi Pref., Sendai, Y. Iokawa 5239.
	Japan, Fukushima Pref., Miyakoji-mura, Y. Iokawa 5237.
	Japan, Fukushima Pref., Yabuki-machi, Y. Iokawa 5241.
<i>Trifolium repens</i>	Japan, Miyagi Pref., Sendai, Y. Iokawa 5243.



Figs. 1–4. Features of trifoliolate leaves at the top of petiole. 1. *Kummerowia striata*. 2. *K. stipulacea*, leaf from lower part of stem. 3. *K. stipulacea*, leaf from upper part of stem. 4. *Trifolium repens*. 1, lateral leaflet; p, petiole; pl, pulvinus of lateral leaflet; pt, pulvinus of terminal leaflet; r, rachis; t, terminal leaflet. Scale bars = 500 μm .

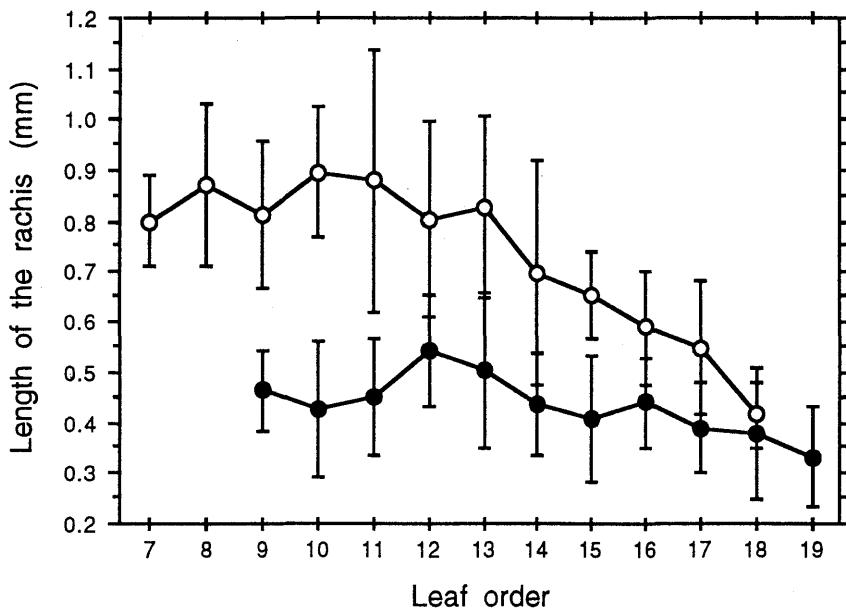


Fig. 5. Variation in length of rachis in relation with order of leaf on main stem. ○: *Kummerowia striata*, ●: *K. stipulacea*. Rachises were measured on fully-formed leaves of 10 individuals in each species. Averages were plotted in each order of leaf, from 7th to 18th in *K. striata* and from 9th to 19th in *K. stipulacea*, because leaves below were lost and above were not fully-formed in some individuals. Vertical bars represent standard deviations. Vouchers: *K. striata* (Y. Iokawa 5239), *K. stipulacea* (Y. Iokawa 5240).

stipulacea. The transverse sections of petiole and rachis have two ridges on the adaxial side (Figs. 6A, 6B, 6C, 7A, 7B, 7C), while that of pulvinus is circular (Figs. 6D, 7D).

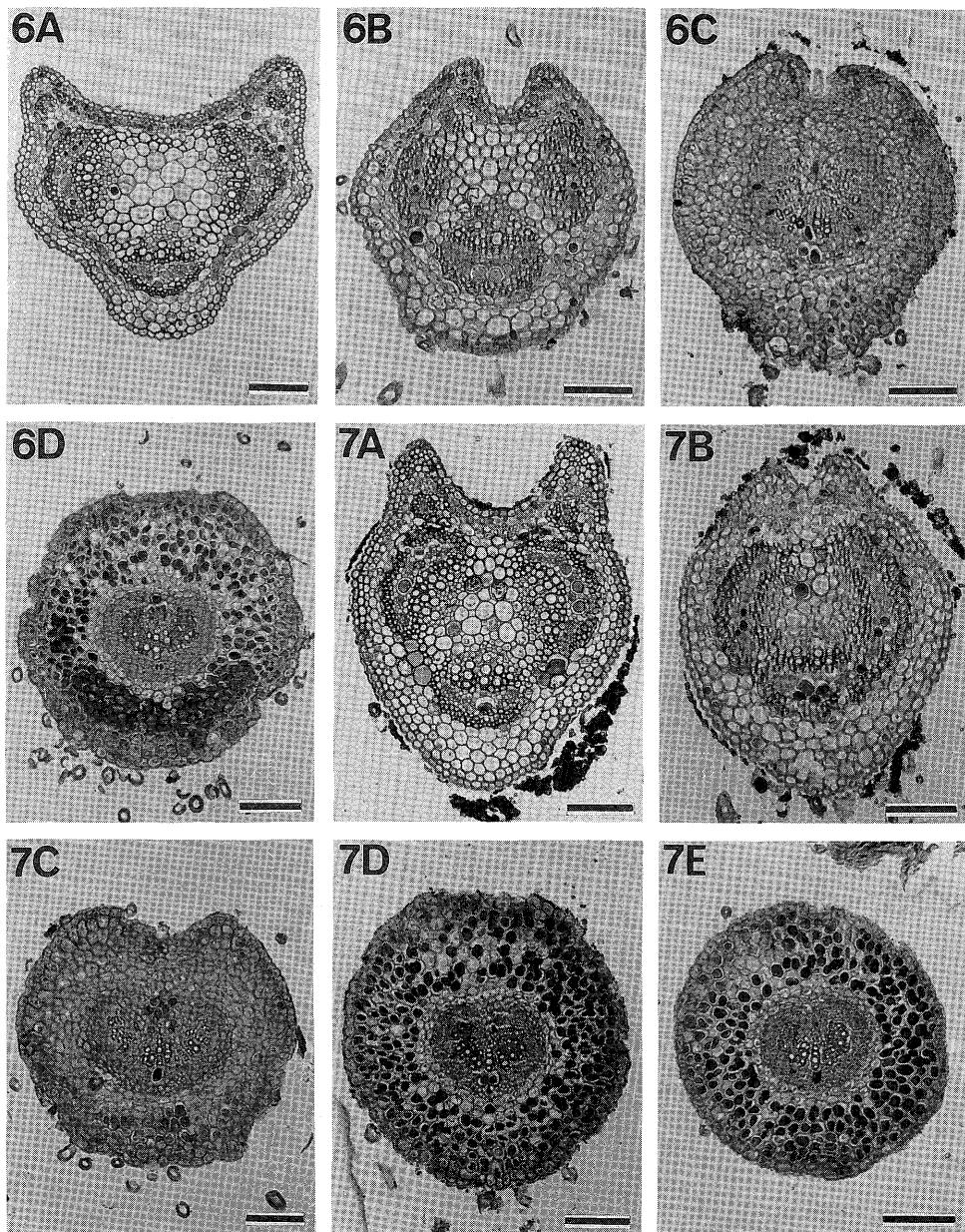
Both species have similar vascular system. The petiole has three major vascular bundles, i.e., a median bundle and a pair of lateral bundles (Figs. 6A, 7A). In the top of petiole, the adaxial part of each lateral bundle enters the pulvinus of each lateral leaflet as a single vascular bundle, the transverse section of which shows a continuous arc (Fig. 7E). The three vascular bundles are kept through the rachis except at the top (Figs. 6B, 7B). At the top of rachis, the three vascular bundles fuse into a single vascular bundle, and the bundle shows a continuous arc and gradually concentrates in the center (Figs. 6C, 7C). This bundle is kept throughout the pulvinus of terminal leaflet (Figs. 6D, 7D). The basal vascular system

in the leaf of *Kummerowia* is shown in Fig. 8A.

When the rachis is very short in upper leaves, it sometimes doesn't have the three vascular bundles but only single vascular bundle because the three vascular bundles fuse together at the top of petiole (Fig. 8B). The whole vascular system in such rachis is similar to that at the top of longer rachis.

Discussion

The rachis is the important morphological characteristic for distinguishing the pinnately trifoliolate leaf from the palmately trifoliolate one. Because each leaflet has the pulvinus at the base throughout the Leguminosae (Dormer 1946), the terminal leaflet is connected by the rachis and pulvinus with the petiole in the pinnately trifoliolate leaf. The rachis has two ridges on the adaxial side in many leguminous leaves (Watari 1934), while the pulvinus has, generally,



Figs. 6-7. Transverse sections of petiole (A), rachis (B), top of rachis (C), pulvinus of terminal leaflet (D) and pulvinus of lateral leaflet (E). 6. *Kummerowia striata*. 7. *K. stipulacea*. Scale bars = 100 μm .

somewhat swollen outline and wrinkled surface (Esau 1977). We could recognize the rachis in the leaf of *Kummerowia* not only by these external features but also by being jointed with the pulvinus of terminal leaflet. Although the rachis becomes shorter in upper

leaves, it is clearly distinguished from the pulvinus by these morphological features. The palmately trifoliolate leaf has no rachis above the petiole (Hickey 1979), as represented by that of *Trifolium repens*. The leaf organization of *Kummerowia* is therefore re-

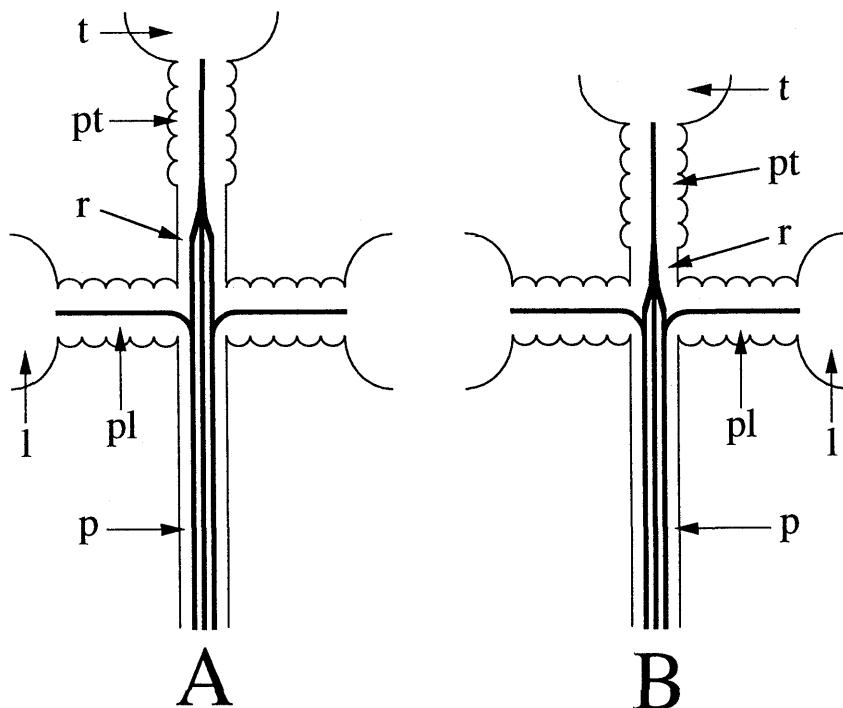


Fig. 8. Diagrams showing vascular system in leaf of *Kummerowia*. A: Lower leaf with longer rachis. B: Upper leaf with shorter rachis. l, lateral leaflet; p, petiole; pl, pulvinus of lateral leaflet; pt, pulvinus of terminal leaflet; r, rachis; t, terminal leaflet.

garded as being pinnately trifoliolate.

Watari (1934) anatomically observed the petioles and rachises of 133 leguminous species, and pointed out the following difference in vascular system between the pinnately trifoliolate leaf and the palmately trifoliolate one: the vascular bundles from the petiole enter the pulvinus of terminal leaflet after passing through the rachis in the pinnately trifoliolate leaf, while they directly enter there in the palmately trifoliolate one. He also pointed out that the rachis of the pinnately trifoliolate leaf usually has three vascular bundles. He regarded the vascular system in the leaf of *K. striata* as that in the palmately trifoliolate leaf.

However, we usually observed three vascular bundles in the rachis of *Kummerowia*, and the vascular system was clearly distinguished from that in the pulvinus of terminal leaflet. The vascular system in

the leaf of *Kummerowia* is, therefore, basically that of the pinnately trifoliolate leaf, although the short rachis of upper leaves sometimes doesn't have three vascular bundles but only single vascular bundle. We suppose that Watari observed upper leaves of *K. striata*. In upper leaves, the vascular system is similar to that of the palmately trifoliolate leaf, because the rachis is not clearly distinguished from the pulvinus of terminal leaflet only by the vascular system. In our anatomical observation, however, the rachis was clearly distinguished from the pulvinus by the shape of the transverse section even in upper leaves, that is, the transverse section of rachis has two ridges on the adaxial side while that of pulvinus is circular. The single vascular bundle is also formed at the top of longer rachis in lower leaves (Fig. 8A). The short rachis of upper leaves, therefore, corresponds with the top of longer rachis. Thus, in addition to morphologi-

cal features, anatomical observations also support the leaf organization of *Kummerowia* to be pinnately trifoliolate.

From our observations, most of lower leaves with longer rachis were found to fall down before flowering. Most of leaves remaining in herbarium specimens with flowers or pods are, therefore, the upper ones which have shorter rachises. Probably, for these reasons, the leaf of *Kummerowia* has often been regarded as being palmately trifoliolate.

Although the leaf organization of *Kummerowia* has been controversial and often distinguished from those of the related two genera, *Lespedeza* and *Campylotropis* (Ohwi 1965, Hatusima 1975, Isely 1990), the present results clarified that the leaf organization of the former is similar to those of the latters. The similarity in the leaf organization is consistent with the closer relationship proposed among these genera (Nemoto and Ohashi 1988, 1990, 1993, 1996, Nemoto et al. 1995).

References

Akiyama S. and Ohba H. 1985. The branching of the inflorescence and vegetative shoot and taxonomy of the genus *Kummerowia* (Leguminosae). *Bot. Mag. Tokyo* **98**: 137–150.

Dormer K. J. 1946. Vegetative morphology as a guide to the classification of the Papilionatae. *New Phytol.* **45**: 145–161.

Esau K. 1977. Anatomy of seeds plants (2nd edn). John Wiley, London.

Fu P. Y. 1987. A study of the genus *Campylotropis* Bunge in China. *Bull. Bot. Res.* **7**: 11–55 (in Chinese).

——— 1995. *Campylotropis*. In: Lee S. K. (ed.), *Flora Reipublicae Popularis Sinicae* **41**: 92–131. Science Press, Beijing (in Chinese).

Hatusima S. 1975. Flora of the Ryukyus. 1002 pp. Okinawa-seibutsukyouiku-kennkyuukai, Naha (in Japanese).

Hickey L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. In: Metcalfe C. R. and Chalk L. (eds.), *Anatomy of the Dicotyledons* (2nd ed.) **1**: 25–39. Clarendon Press, Oxford.

Howard R. A. 1979. The petiole. In: Metcalfe C. R. and Chalk L. (eds.), *Anatomy of the Dicotyledons* (2nd ed.) **1**: 88–96. Clarendon Press, Oxford.

Hutchinson J. 1964. Tribe Lespedezeae. In: *The Genera of Flowering Plants* **1**: 486–489. Oxford University Press, London.

Isely D. 1990. Vascular Flora of the Southeastern United States **3**, 258 pp. The University of North Carolina Press, Chapel Hill.

Li J. Y. and Chen Y. A. 1995. *Lespedeza*. In: Lee S. K. (ed.), *Flora Reipublicae Popularis Sinicae* **41**: 131–159. Science Press, Beijing (in Chinese).

Liu Y. 1955. *Kummerowia*. In: *Flora Illustralis Plantarum Primarum Sinicarum*, pp. 544–546. Science Press, Beijing (in Chinese).

Nemoto T. and Ohashi H. 1988. Floral nectaries in *Lespedeza*, *Kummerowia* and *Campylotropis* (Leguminosae). *J. Jpn. Bot.* **63**: 48–62, pls. IV–IX.

——— and ——— 1990. Organographic and ontogenetic studies on the inflorescence of *Lespedeza cuneata* (Dum.-Cours.) G. Don (Leguminosae). *Bot. Mag. Tokyo* **103**: 217–231.

——— and ——— 1993. The inflorescence structure of *Kummerowia* (Leguminosae). *Bot. J. Linn. Soc.* **111**: 281–294.

——— and ——— 1996. The inflorescence structure of *Campylotropis* (Leguminosae). *Amer. J. Bot.* **83**: in press.

———, ——— and Tamate H. 1995. Phylogeny of *Lespedeza* and its allied genera (Desmodieae-Lespedezinae). In: Crisp M. and Doyle J. J. (eds.), *Advances in Legume Systematics* **7**: 351–358. Royal Botanic Gardens, Kew.

Ohashi H., Polhill R. M. and Shubert B. G. 1981. Desmodieae. In: Polhill R. M. and Raven P. H. (eds.), *Advances in legume systematics* **1**: 292–300. Royal Botanic Gardens, Kew.

Ohwi J. 1965. Flora of Japan. 1067 pp. Smithsonian Institution, Washington, D.C.

Watari S. 1934. Anatomical studies on some Leguminous leaves with special reference to the vascular system in petioles and rachises. *J. Fac. Sci. Imp. Univ. Tokyo, Sec. III, Botany* **4**: 225–365.

Yang Y. C. and Huang P. W. 1995. *Kummerowia*. In: Lee S. K. (ed.), *Flora Reipublicae Popularis Sinicae* **41**: 159–161. Science Press, Beijing (in Chinese).

五百川裕, 根本智行, 大橋広好: マメ科ヤハズソウ属の葉形

マメ科ヤハズソウ属の葉形は、3出掌状複葉あるいは3出羽状複葉とされる。本研究では、ヤハズソウ属の葉形の形態学的および解剖学的な再検討を試みた。その結果、葉柄先端と頂小葉の小葉枕との間に、短い葉軸が存在することが明らかと

なった。葉軸は向軸側に2本の稜を持ち表面にしわのないことで、小葉枕から容易に区別できる。葉軸は植物体下部につく葉では明瞭に認められるが、上部の葉ではかなり短くなる。顯著な葉軸を持つ下部の葉の多くは、花時までに脱落し、おし

葉標本に残りにくいことが、ヤハズソウ属の葉形がしばしば3出掌状複葉とされた理由と考えられる。また、葉柄、葉軸、小葉枕における維管束走向も、これまでに報告されている他のマメ科の種の3出羽状複葉における維管束走向と基本的に一

致した。したがって、ヤハズソウ属の葉形は、3出羽状複葉であり、近縁とされるハギ属、ハナハギ属の葉形と共通することが明らかとなった。

(東北大学大学院理学研究科生物学教室)